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TOP-DOWN CONTROL OF SMALL HERBIVORES ON SALT-MARSH VEGETATION ALONG A PRODUCTIVITY GRADIENT

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Abstract. Exploitation theory predicts strongest plant–herbivore interactions at sites of intermediate productivity. Recent studies illustrate the importance of top-down effects by small to intermediate-sized herbivores in structuring salt-marsh communities. How long-term effects of herbivory are modified by productivity of the system is a largely unexplored area. We studied how herbivory by geese and hares affected plant species replacement by erecting exclosures along a natural productivity gradient in a temperate salt-marsh system. After seven years, the largest shifts in species composition were observed when both hares and geese were excluded from plots. Only excluding geese did not have a large impact on species replacement, indicating that geese alone did not control the vegetation. Herbivory slowed down succession by retarding the establishment and spread of late-successional species on the low salt marsh. Effects of herbivory were less clear on the high marsh. Vegetation change after excluding herbivores was most pronounced in the most unproductive regions of the salt marsh. As a result, different successional trajectories emerged when herbivores were absent or present at the onset of salt-marsh succession. At sites of intermediate productivity, where grazing pressure was highest, no effect of herbivory on species composition was found. We hypothesize that the high dominance of grazing tolerant species at these sites retarded the invasion of late-successional species. The intensity of herbivory did not accurately predict the importance of herbivory in structuring plant communities. To understand herbivore effects along productivity gradients, the selectivity patterns of the herbivores and the bottom-up effects of plants on these interactions need to be considered.

Key words: *Atriplex portulacoides*; *Barnacle Goose*; *Brent Goose*; *Elymus athericus*; *hare*; *succession*.

INTRODUCTION

Top-down control is important in structuring plant communities (Hairston et al. 1960), and is predicted to increase along a gradient of primary productivity (Fretwell 1977, Oksanen et al. 1981, DeAngelis 1992). At sites of low productivity, plant biomass is too low to support a herbivore population and plants will be regulated by bottom-up effects (e.g., nutrient availability). Top-down regulation of plant biomass by herbivores will occur at sites of intermediate levels of productivity. Plants are predicted to escape from this regulation at sites where higher levels of productivity occur. At these sites herbivores themselves will be top-down regulated by carnivores (Oksanen and Oksanen 2000). The “quality threshold hypothesis” (Van de Koppel et al. 1996, Olff et al. 1997, Huisman et al. 1999) states that bottom-up effects can play an equally important role at highly productive sites. This hypothesis predicts that herbivore grazing pressure can decrease, even in the absence of carnivores, at sites where high productivity occurs. Declining forage quality at high plant standing crops, due to changing species composition and an increase in the C:N ratio, may explain the decreasing

herbivore density. Despite the different mechanisms, both hypotheses predict that the strongest herbivore–plant interactions will occur at sites of intermediate productivity.

Recent studies stress the importance of top-down effects in salt-marsh communities. In addition to the effects of large grazers, such as livestock (e.g., Turner 1987, Bos et al. 2002, Bakker et al. 2003), studies on American salt marshes illustrate that small to intermediate-sized herbivores can regulate plant growth. For instance, grazing by insects (Bertness et al. 1987, Bertness and Shumway 1992), crabs (Bortolus and Iribarne 1999), snails (Silliman and Zieman 2001, Silliman and Bertness 2002), and Greater Snow Geese (Smith and Odum 1983) can regulate plant production in *Spartina*-dominated salt marshes. When herbivores strongly influence species composition and productivity, changes in vegetation composition and biomass are predicted when grazing pressure is relaxed (Oksanen et al. 1981). Preventing grazing by Lesser Snow Geese in an Arctic salt marsh system led to large changes in the plant community, and showed that goose grazing retarded succession (Bazely and Jefferies 1986, Hik et al. 1992). Studies in temperate salt marshes also show the potential importance of intermediate-sized herbivores, such as geese (Bazely and Jefferies 1986, Hik et al. 1992, Zacheis et al. 2001) and hares (Van der

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Wal et al. 2000c) in structuring the vegetation. Although the effects of top-down control are predicted to change with primary productivity of the system, few studies have looked at how the effects of herbivory are modified by increased primary productivity within a single system, such as a salt marsh (Dormann et al. 2000, Van der Wal et al. 2000a, Silliman and Zieman 2001).

Although the model of exploitation theory (Fretwell 1977, Oksanen et al. 1981, DeAngelis 1992) is based on a large-scale comparison of systems differing in primary productivity (see also Oksanen and Oksanen 2000), we tested whether we can apply these predictions on a small-scale productivity gradient. The salt marsh at the island of Schiermonnikoog in the Dutch Wadden Sea supports a natural productivity gradient and, therefore, offers the opportunity to test how intermediate-sized herbivores affect the community structure with increasing primary productivity. The major herbivores (geese, hares and rabbits) do not have predators and show a peak in grazing pressure at sites of intermediate productivity (Van de Koppel et al. 1996). The increasing abundance of tall, relatively unpalatable plant species with increasing productivity of the salt marsh causes a decrease in grazing pressure at older, more productive sites (Van de Koppel et al. 1996, Olff et al. 1997, Huisman et al. 1999). This implies that herbivores are evicted from sites as a result of vegetation succession and do not influence directly the plant species replacement (Van der Wal et al. 2000b). However, Van der Wal et al. (2000c) showed that hares can prevent the spread of a typical late-successional species for several decades. We extended this study and investigated how grazing influenced overall species composition and vegetation succession on high and low salt marshes along this natural productivity gradient. As we were concerned with multiple species of herbivores, we examined which was most important; spring-grazing geese or year-round-grazing hares and rabbits.

We hypothesized that when herbivory directly influenced the species composition of the vegetation and retarded succession, release of herbivore control should lead to on-going succession. As strongest plant-herbivore interactions were expected at sites where intermediate levels of productivity occurred, the largest changes in plant species composition were expected at these sites when herbivory is excluded.

METHODS

Study site

The experiment was conducted in the salt marsh of the island of Schiermonnikoog, in the Dutch Wadden Sea (53°30' N, 6°10' E). Due to the eastward expansion of this island, a series of salt marshes at different developmental stages can be found adjacent to each other (Olff et al. 1997). Clay layer thickness and hence ni-

trogen content of the soil increases with marsh age (Olff et al. 1997, Van Wijnen and Bakker 2000). As a consequence, the chronosequence features a natural productivity gradient (Van de Koppel et al. 1996). Each elevation class in the salt marsh shows a distinctive pattern of species replacement (Olff et al. 1997). The lower elevations of young marshes are dominated by small-statured pioneer species, such as *Salicornia europaea*, *Puccinellia maritima*, *Suaeda maritima*, and *Spergularia maritima*. These are replaced by the taller species *Festuca rubra* and *Plantago maritima* at the intermediate stages. The shrub *Atriplex portulacoides* and the tall grass *Elymus athericus* dominate the older stages. At higher elevations of the salt marsh, early-successional species such as *Festuca rubra* are replaced by tall growing species, such as *Elymus athericus* and *Artemisia maritima* at the older sites. The salt marsh is intensively grazed by spring staging Brent Geese (*Branta bernicla*) and Barnacle Geese (*Branta leucopsis*) (Stahl et al. 2001). Brown hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) are present year-round at the salt marsh. Carnivores are absent from this island. The study area has never been grazed by livestock.

Experimental design

Four salt marsh sites, differing in age since their inception, were selected along the chronosequence. The age of each site was determined by aerial photographs that were taken at different times of the study area. The time when vegetation first started to develop was used as the starting point of the salt marsh development (for further details see Olff et al. 1997). The sites were one, eight, 20, and 30 years old when the experiments began. Clay layer thickness increased with site age (Table 1). As a result of increased soil nutrient levels, the canopy height of the vegetation increased and the amount of bare soil decreased with site age. At each site, four exclosures were erected in October 1994: two in the high marsh and two in the low marsh (see Table 1). The exclosure sites coincided with the transects studied by Olff et al. (1997). Every exclosure plot contained three treatments. Controls were freely accessible to geese and hares. Goose exclosures (7 × 7 m), excluded geese by two metal wires strung at 20 and 50 cm above the soil and allowed hares to enter freely. Full exclosures (at least 7 × 7 m), excluded both hares and geese by a 1 m high chicken-wire fence, and ropes suspended at a height of 50 cm to prevent geese from flying into the fenced area. Dropping counts showed that the treatments successfully excluded geese (in the goose exclosures) and both geese and hares (in the full exclosures). In each treatment, four permanent quadrats (of 2 × 2 m) were established, resulting in 24 quadrats both at the low and at the high marsh at each site. In each quadrat, vegetation composition was measured every year (in August or September) from 1995 to 2001. Cover of each plant species and bare soil was estimated

TABLE 1. Characteristics of the sites where the exclosures have been established since 1994.

Marsh type	Age of marsh (yr) [†]	Cover of bare soil (%) [n = 24]	Canopy height (cm) [n = 32]	Clay thickness (cm) [n = 48]	Elevation (m + MHT) [‡] [n = 20]
High	1	70.9 ^a ± 3.0	12.5 ^a ± 0.6	0.2 ^a ± 0.5	0.71 ^a ± 0.04
	8	0 ^b ± 0	24.6 ^b ± 1.1	3.2 ^b ± 0.9	0.86 ^a ± 0.04
	20	0.4 ^b ± 0.4	23.5 ^b ± 1.6	3.9 ^b ± 0.7	0.72 ^a ± 0.02
	30	0.8 ^b ± 0.6	39.3 ^c ± 1.6	6.3 ^c ± 2.9	0.80 ^a ± 0.05
Low	1	90.9 ^a ± 1.3	3.2 ^A ± 0.5	3.1 ^A ± 0.5	0.13 ^A ± 0.004
	8	15.8 ^b ± 2.6	21.2 ^B ± 0.5	5.9 ^B ± 1.2	0.32 ^B ± 0.008
	20	4.2 ^c ± 1.5	22.8 ^B ± 0.5	12.9 ^C ± 1.1	0.41 ^C ± 0.009
	30	1.2 ^c ± 1.0	26.5 ^C ± 1.7	10.6 ^D ± 0.9	0.35 ^D ± 0.007

Notes: Significant differences are indicated with different letters (capital letters for low salt marsh), based on Tukey's multiple comparison tests ($P < 0.05$). Cover of bare soil was measured when exclosure were established; canopy height was measured three years later. Cover of bare soil, canopy height, and clay thickness were measured inside the exclosure treatments, and elevation was measured in close vicinity of the exclosures and was expressed relative to mean high tide. Values are means ± 1 SE.

[†] Age of marsh at the time when exclosures were erected.

[‡] Mean high tide.

using the decimal scale of Londo (1976). Plant species nomenclature follows Van der Meijden et al. (1990). Permanent quadrats were at least 50 cm away from a fence to exclude fence effects. Canopy height of the vegetation was measured in June 1996 inside the full exclosures by dropping a styrofoam disc (19 cm diameter, 20 g) along a calibrated stick, on to the vegetation. Elevation (relative to MHT) was measured by means of a theodolite in June 2001 in the area between the exclosures. Clay thickness in every quadrat was measured by means of a soil corer to the nearest centimeter in June 2001.

Grazing pressure

Dropping density is a good estimate of the amount of grazing by geese (Owen 1971) and hares (Langbein et al. 1999). At each site, a transect of 20 plots of 4 m² each was established, starting at the foot of a dune and ending at the low salt marsh. The transects thus covered the entire gradient from high to low salt marsh. The distance between each plot was at least 10 m. Drop-pings were counted and removed every second week from October 1999 to September 2000. In order to compare the grazing pressure of geese, hares, and rabbits, the biomass removed by each herbivore was calculated using the method described by Van de Koppel (1997). Consumption (C), expressed as total amount of biomass removed by geese and hares, was estimated by dividing the total fecal mass (FM) by one minus the digestive efficiency (DE), or $FM/(1 - DE)$. Values of dropping dry mass (geese, 0.85 g per dropping; hare, 0.15 g per dropping) and digestive efficiency (Brent Goose, 35% dry matter digestibility; hare, 65%) were obtained from literature (Van der Wal et al. 1998). In order to compare grazing pressure between sites, total biomass removed by all herbivores was summed and expressed as a percentage of the maximum potential standing crop of each area. Potential standing crop was

calculated as the maximum standing crop values of a salt marsh with a certain age (taken from Van de Koppel et al. 1996) and the biomass removed by the herbivores.

Data analysis

Differences between sites in clay thickness, elevation, canopy height, and grazing pressure by each herbivore were analyzed using Tukey tests. The effects of treatment on the cover of individual plant species were tested for each exclosure with a Tukey test. A selection of plant species was made. Results of all species are presented in Appendices A and B. The selected species dominated the vegetation and represented most of the biomass at a certain successional stage. In the high marsh, the early-successional species *Festuca rubra* was compared to the late-successional *Elymus athericus*. In the low marsh, the early-successional species *Salicornia europaea* and *Puccinellia maritima* were compared to the mid-successional species *Plantago maritima* and *Festuca rubra* and the late-successional species *Atriplex portulacoides* and *Elymus athericus*. The effects of herbivory on the community structure were analyzed using a multivariate approach for the high and the low marsh separately. The change in cover of each plant species between 1995 and 2001, was log transformed in order to prevent the most abundant plant species from unduly dominating the ordination (Jongman et al. 1995). Treatment effects were tested using RDA (redundancy analysis), as the gradient length was smaller than two standard deviations (Jongman et al. 1995). Treatments (control, goose, full) were entered as environmental data, and the two exclosures as covariables. Exclosures were classified as blocks, as the replicate quadrats of each treatment in an exclosure are pseudoreplicates (Hurlbert 1984). The significance of effects was tested using Monte Carlo permutation tests, allowing permutations between treatments within each exclosure. A step-forward procedure was used. The

TABLE 2. Biomass consumption by geese, hares, and rabbits in salt marshes of different ages.

Age of marsh (yr)	Consumption (g dry mass·m ⁻² ·yr ⁻¹)			Biomass removed (%)
	Goose <i>n</i> = 20	Hare <i>n</i> = 20	Rabbit <i>n</i> = 20	
1	18.7 ^a ± 1.4	5.0 ^a ± 1.6	0.2 ^a ± 0.2	13.4 ^a ± 1.1
8	27.3 ^b ± 2.9	11.6 ^a ± 3.6	1.0 ^a ± 0.4	15.8 ^a ± 1.9
20	28.2 ^b ± 1.7	26.9 ^b ± 4.2	1.1 ^a ± 0.5	17.9 ^a ± 1.3
30	13.3 ^a ± 1.5	5.5 ^a ± 1.4	0.01 ^a ± 0.01	6.2 ^b ± 0.8

Notes: Consumption is calculated on the basis of cumulative droppings collected throughout the year on plots at each site; see *Methods* for further details. Total consumption of all three herbivores is calculated and expressed as a percentage of the maximum standing crop biomass at each site. Values are means ± 1 SE. Different letters indicate significant differences ($P < 0.05$).

direction of vegetation change was analyzed using a detrended correspondence analyses (DCA), as the gradient length was larger than four standard deviations (Jongman et al. 1995). Species cover data was not transformed. The centroids of each treatment and species in 1995 and 2001 were plotted in a diagram to show the change in ordination space.

RESULTS

Consumption by herbivores

Goose grazing removed the largest amount of biomass in the 1-, 8- and 30-yr-old marshes (Tukey tests, $P < 0.0001$) compared to that of hare and rabbit grazing (Table 2). In the 20-yr-old marsh, equal amounts were removed by both goose species compared to that grazed by hares alone (Tukey test, $P = 0.93$). Biomass removal by rabbits was significantly lower than that of the other

herbivores at each site ($P < 0.02$). All herbivores showed a maximum in the amount of grazing in the 20-yr-old marsh. When total consumption was expressed as a percentage of the potential standing crop that was removed by all herbivores, there were no significant difference between the 1-, 8- and 20-yr-old marshes, but proportional consumption decreased at the 30-yr-old marsh.

Treatment effects of exclosures

Overall effects of treatments on the high and low salt marshes for each exclosure were analyzed by multivariate analyses. The RDA showed that the full and goose exclosures explained a significant part of the shift in plant species composition meaning that the shift in species composition is significantly affected by these treatments (Table 3). On the high marsh the results from the full exclosures showed a different shift in species composition in the marsh of one, 20 and 30 years old compared to the goose exclosures and control plots. The results from the goose exclosures did not explain a significant part of this variation. On the low marsh, the full exclosures explained most of the variation in the shift in species composition. Species replacement was significantly affected in the marshes of one, eight, and 30 years of age, but not in the 20-yr-old marsh. Results from the goose exclosures explained an additional part of the variation in one site only (8-yr-old marsh). The highest percentage of the variation in species change in the low salt marsh occurred at the youngest site. As the overall treatment effects on the vegetation were significant, it is legitimate to examine the effects on individual plant species.

Effect of treatments on individual species

The change in species cover in the high marsh did not show consistent responses to treatments when both exclosures were compared (Fig. 1). In the youngest marsh (one year), *Festuca rubra* showed the largest increase in both full exclosures. At all but the youngest site, *Elymus athericus* increased at the expense of *Festuca rubra* irrespective of treatment. Sites which show the largest increase in *Elymus*, also showed the largest decrease in *Festuca*.

TABLE 3. Results from the RDA (redundancy analysis) showing the effects of the different types of exclosures at each site in the low and high salt marshes.

Marsh type	Age of marsh (yr)	Treatment	<i>F</i>	<i>P</i>	Variance explained (%)
High	1	full	2.879	0.004	70.1
		goose	1.207	0.239	
	8	full	1.527	0.101	68.1
		goose	1.527	0.088	
	20	full	3.137	0.001	75.9
		goose	1.511	0.082	
Low	30	full	3.892	0.001	83.1
		goose	1.261	0.241	
	1	full	5.356	0.001	68.1
		goose	1.095	0.329	
	8	full	4.665	0.001	31.9
		goose	2.129	0.023	
	20	full	1.350	0.193	69.5
		goose	1.251	0.222	
	30	full	3.305	0.001	
		goose	1.485	0.142	

Notes: Significance levels were tested with Monte Carlo permutation tests. The percentage of the total variance in plant species composition that is explained is shown for the treatments that had a significant effect. *P* values indicate whether adding a treatment to the model explained a significantly higher percentage of the variance compared to a simpler model. Degrees of freedom were 2, 21 for all *F* tests.

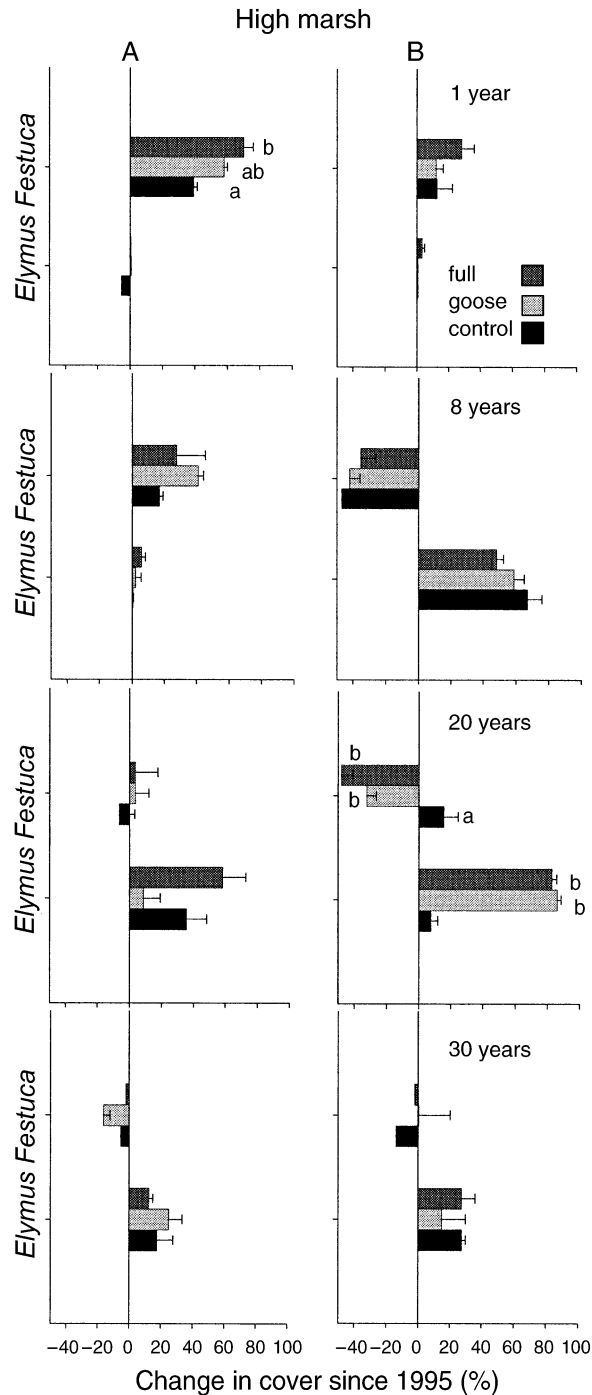


FIG. 1. Increase and decrease of typical early- and late-successional plant species in change of percent cover between 1995 and 2001 on the high marsh (results of all species are presented in Appendices A and B). The two exclosures (A and B) are depicted separately. Change in percent cover (mean ± 1 SE) is calculated from the four permanent quadrats in each treatment. The early-successional *Festuca rubra* is compared to the late-successional *Elymus athericus*. Different letters beside error bars denote significant differences between treatments in plant species cover. When no letters are present, there are no significant effects of treatment.

The effects of the treatments on the species composition in the low salt marsh were more pronounced than those in the high salt marsh (Fig. 2). Typical plant species that increased in cover in both full exclosures at the 1-yr-old marsh were *Atriplex portulacoides* and *Festuca rubra*, whereas *Salicornia europaea* increased the least compared to the other treatments. *Elymus athericus* is a typical late-successional species that cannot be found in the area surrounding the exclosures at the young marsh site. However, it has become established and is increasing in abundance in both the full exclosures at this site. As there are only a few individual plants, the cover is low (less than 1%). In the control plots, *Puccinellia maritima* showed the largest increase. At the 8-yr-old marsh, *Festuca rubra* increased mostly in the full exclosures at the expense of *Puccinellia maritima*. The goose exclosures showed a shift in species composition that was intermediate between the full and the control treatments. Only one species at one of the two exclosures was significantly affected in the 20-yr-old marsh. At the oldest site (30 years) the two full exclosures showed different patterns of shift in species composition. In one exclosure, *Elymus athericus* increased at the expense of *Atriplex portulacoides* and today the vegetation at this site shows a high dominance of *Elymus athericus*. The other exclosure showed an increase in the cover of *Atriplex portulacoides* and is at present largely dominated by *Atriplex portulacoides*.

Direction of change in plant species

When all permanent quadrats of the high marsh were plotted on a DCA diagram (Figs. 3A and 4A), plant species that are typical of early-successional stages, such as *Elymus farctus*, *Parapholis strigosa*, and *Amphiphila arenaria*, were located in the left side of the diagram. Species that typically dominate late-successional stages, such as *Elymus athericus* and *Atriplex prostrata* are on the right side of the diagram. Fig. 4 shows how the centroids of each treatment at each site changed in ordination space. The starting position of the treatments at each site is necessarily different, as they had a different species composition when the exclosures were erected. The centroids of the youngest site moved in the direction of increasing cover of *Festuca rubra*, whereas all other centroids moved towards increased cover of *Elymus athericus*. The magnitude of change did not show consistent differences between treatments, as indicated by the lengths of the arrows. Only the full exclosure in the 20-yr-old marsh showed larger changes than those in the distribution of the other treatments. Plant species, which are typical for early-successional stages of the low marsh, such as *Salicornia europaea*, *Spergularia maritima*, *Suaeda maritima*, and *Spartina anglica* were on the left side of the DCA-diagram (Fig. 3B). Species that typically dominate late-successional stages, such as *Elymus athericus* and *Festuca rubra*, were placed in the right side of the diagram.

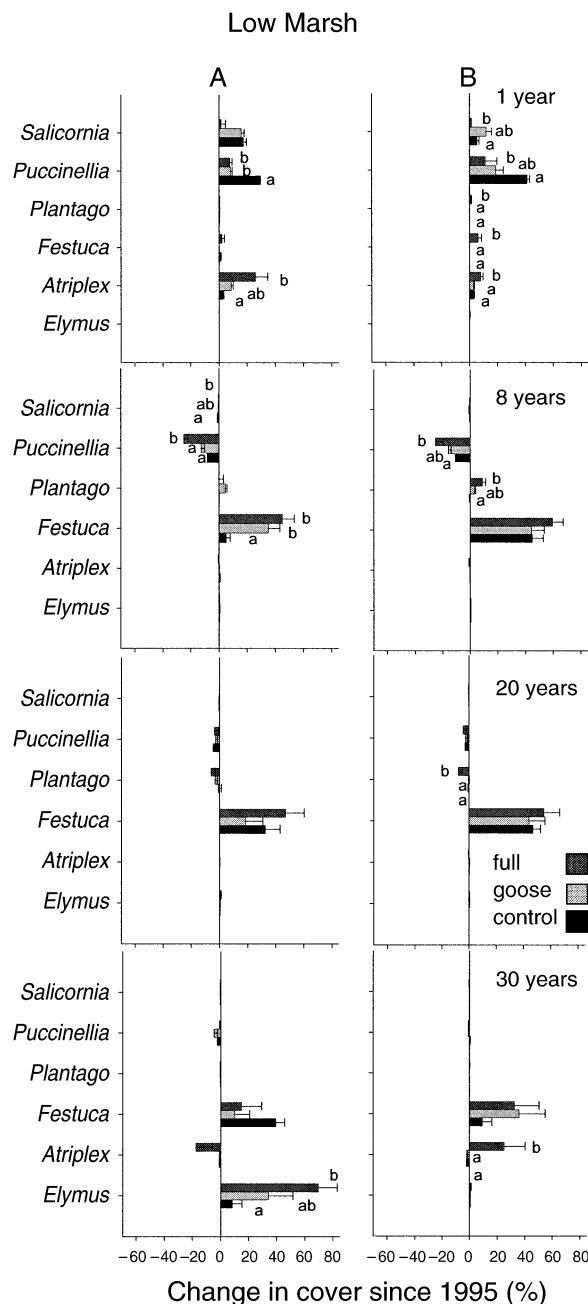


FIG. 2. Increase and decrease of typical early- and late-successional plant species in change of percent cover between 1995 and 2001 on the low marsh (results of all species are presented in Appendices A and B). The two exclosures (A and B) are depicted separately. Change in percent cover (mean \pm 1 SE) is calculated from the four permanent quadrats in each treatment. The early-successional *Salicornia europaea* and *Puccinellia maritima* are compared to the mid-successional *Plantago maritima* and *Festuca rubra* and the late-successional *Atriplex portulacoides* and *Elymus athericus*. Different letters beside error bars denote significant differences between treatments in plant species cover. When no letters are present, there are no significant effects of treatment.

All treatments showed a similar direction in the shift in species composition, they moved in the direction of increasing cover of the late-successional species, and decreasing cover of early-successional species (Fig. 4B). The marshes that are eight, 20, and 30 years old all converged to the same point, indicating that all sites started to resemble each other in species composition. The vectors for the full exclosures were larger than those of the controls and goose exclosures at each site, except for the 8-yr-old marsh, indicating larger changes in species cover. The largest difference in the results between the full exclosure and other treatments was found at the 1-yr-old marsh. Here, especially in the full exclosure, the vegetational cover shifted towards a higher cover of *Atriplex portulacoides*, whereas all other sites showed an increased cover of *Festuca rubra* and to a lesser extent *Elymus athericus*.

DISCUSSION

The main conclusion of this study is that intermediate-sized herbivores, such as hares, can play an important role in structuring salt-marsh communities. Although total consumption of forage was highest at intermediate productive stages, the impact of grazing on vegetation succession was highest at unproductive, young successional stages. Grazing prevented the establishment of typical late-successional species and retarded successional processes for several decades.

Goose and hare herbivory

Species change at only one site in the low marsh was affected by goose exclusion, all other sites in the low marsh and all sites in the high marsh were not significantly affected. This shows that geese alone do not have a large impact on successional development in the salt marsh, but the combined effects of grazing by geese, hares, and rabbits does have an impact. Other studies have observed that goose grazing strongly affected species composition and retarded vegetation succession in an Arctic salt marsh (Bazely and Jefferies 1986, Hik et al. 1992). An important difference between the Arctic system and our temperate marsh is the timing of grazing. At our study site, geese graze mainly in spring at the start of plant growth, whereas grazing occurs during the entire growing season in the Arctic. We observed that spring grazing retarded the start of plant growth, but the difference in biomass between goose grazed and ungrazed vegetation disappeared during the growing season (D. J. P. Kuijper, *personal observation*), indicating that plants compensate for these early-season grazing. Another important factor is the way geese graze. As Arctic Snow Geese grub and hence damage the root system of plants, their effects might be more drastic than the grazing on aboveground plant parts by the goose species in our study (Zacheis et al. 2001). Other studies in temperate European salt marshes observed that goose grazing retarded succession in the initial stages of salt-marsh de-

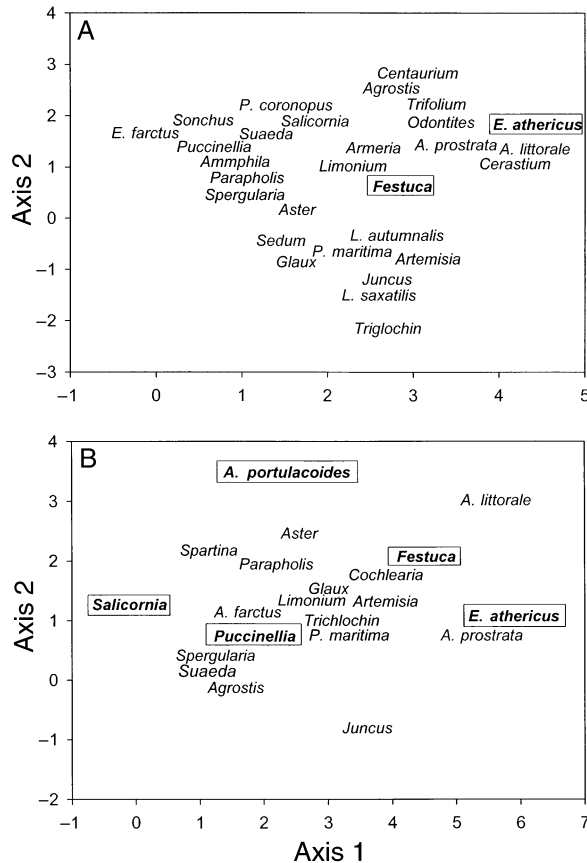


FIG. 3. Biplot of sample and species scores from the detrended correspondence analysis (DCA) showing (A) the relative positions of all plant species on the high salt marsh and (B) on the low marsh along the first two canonical axes. Species are referred to by genus name unless more than one species per genus occurs; then the full name is given. Note the difference in scale between panels (A) and (B).

velopment (Joenje 1985, Rowcliffe et al. 1998). The present study suggests that these effects are no longer visible over longer time scales.

Exclusion of hares, rabbits, and geese accounted for most of the variation at all sites, indicating that hares and rabbits do influence vegetation succession. However, we think that rabbit grazing has no large effect on the salt-marsh vegetation, as total consumption of biomass by rabbits is low (more than 10 times smaller) compared to that of hares. As rabbit grazing is most intense in close vicinity to their burrows (Palomares and Delibes 1997), and no burrows were within 100 m of our plots, the effect of excluding lagomorphs at the low marsh can largely be attributed to hare grazing.

Two factors seem to be important in understanding why hare grazing is more important than goose grazing. First, hares are present year-round and graze during the entire growing season in contrast to migratory geese. Second, although hares and geese have a large overlap

in spring diet choice (Van der Wal et al. 1998), the diet of hares changes in winter (Van der Wal et al. 2000c). In spring, mainly early-successional, grazing-tolerant species are selected, such as *Festuca rubra*, *Puccinellia maritima*, *Triglochin maritima*, and *Plantago maritima*. However, in winter, hares eat late-successional woody species, such as *Atriplex portulacoides*, which are more sensitive to grazing (Van der Wal et al. 2000c).

Herbivory and succession

During undisturbed succession in high temperate European salt marshes, the small-statured plant species, *Festuca rubra*, ultimately will be replaced by the tall-growing grass, *Elymus athericus* (Leendertse et al. 1997, Bos et al. 2002, Bakker et al. 2003). Cover of *Festuca rubra* increased in the present study at the youngest sites (one and eight years old) only, whereas, *E. athericus* increased at all other sites at the expense of *F. rubra*. Although both species were affected when herbivores were excluded, the exclosures at these sites

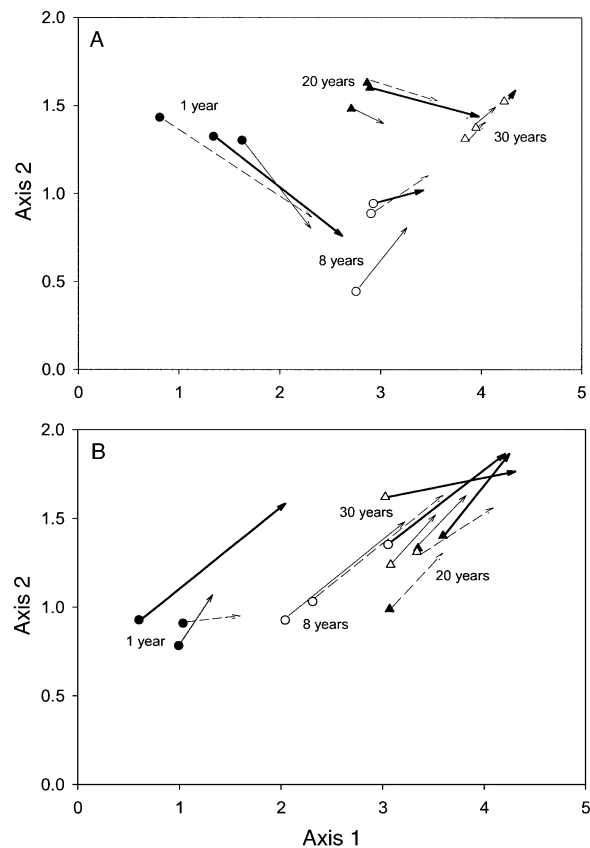


FIG. 4. The change of position of the centroids of the quadrats in the ordination diagram between 1995 and 2001 is shown by arrows on (A) the high marsh and (B) the low marsh. Note the difference in scale between panels (A) and (B). Treatments are indicated by thick lines (full), thin lines (control), and dashed lines (goose). Sites of different ages are indicated by different symbols: solid circle, 1-yr-old; open circle, 8-yr-old; solid triangle, 20-yr-old; and open triangle, 30-yr-old marsh.

showed differential effects with respect to plant cover. This means that grazing by intermediate-sized herbivores may have local effects, but, in general, the grazers are not able to prevent the increase of *Elymus athericus* in the high marsh. As *E. athericus* is not preferred by any herbivore (Prins and Ydenberg 1985, Prop and Deerenberg 1991, Van der Wal et al. 2000c), grazing pressure is low once this species dominates the vegetation.

Undisturbed vegetation succession in the low salt marsh will ultimately result in the dominance of *Atriplex portulacoides* (Leendertse et al. 1997). As grazing pressure is greater in the low marsh (Olf et al. 1997), the effects of excluding herbivores were also more pronounced in the low marsh than in the high marsh. All plots in the low marsh developed in the same floristic direction, as the species composition in younger sites started to resemble older sites (Fig. 4). In general, the cover of species from later successional stages increased, and the cover of species from earlier successional stages decreased more rapidly inside the full exclosures. This shows that herbivory can delay the rate of vegetation succession but cannot arrest it (see also Bazely and Jefferies 1986, Hik et al. 1992). The increasing productivity as a result of continuous sedimentation of clay, causes irrevocable vegetation change (Van Wijnen and Bakker 1999). In the 1-yr-old salt marsh, *Atriplex portulacoides* and *Festuca rubra* increased more rapidly when herbivory was excluded compared to grazed plots. Olf et al. (1997) showed that *F. rubra* had the highest frequency in marshes of 35 and 100 years of age and *A. portulacoides* in marshes of 35 and 60 years of age. Species that are typical of young salt marshes, such as *Puccinellia maritima* and *Salicornia maritima* (Olf et al. 1997), increased more in grazed areas. Although the species are different, a similar development was observed in the 8- and 30-yr-old marshes. In the 8-yr-old marsh, the early-successional species *Puccinellia maritima* decreased at the expense of the later successional *Festuca rubra* inside the exclosures. At the 30-yr-old site, the vegetation inside the exclosures was dominated by *E. athericus* or *A. portulacoides*, both of which are characteristic of the late stages of salt-marsh succession. In the 20-yr-old marsh, where total herbivore consumption was highest, the late-successional species did not increase inside the exclosures. How can this be explained?

The intermediately productive sites, with a high grazing pressure, are characterized by a closed canopy and a high dominance of grazing-tolerant grasses (mainly *Festuca rubra*). When exclosures were established at these sites, the closed canopy might have prevented the establishment of late-successional species by reduced light availability at ground level (Bakker and De Vries 1992) or by lack of bare soil (Gross and Werner 1982). Open vegetation in young unproductive marshes offers the opportunity for the establishment of

late-successional species as long as the selective grazing by herbivores is prevented. The quick establishment of typical late-successional species at the youngest site inside the exclosures supports this view. Once these species have established they will spread more rapidly in the absence of herbivory, indicating that actual establishment is the limiting factor in this invasion and herbivory can retard further spread. This was illustrated at the oldest site (30 years old), where *E. athericus* and *A. portulacoides* both had a high frequency of occurrence at the time when the exclosures were erected, and both increased rapidly when herbivores were absent.

Grazing by intermediate-sized herbivores in this salt-marsh system will thus lead to a different trajectory of succession. In the absence of herbivores, the late-successional plant species can directly invade, during the "window of opportunity" in young marshes, and will dominate the vegetation at an earlier stage. When herbivores are present, the vegetation will develop into a stage where grazing-tolerant plant species dominate at the intermediate productive stages of succession. The closed canopy can prevent the establishment of late-successional species. The top-down effects of the herbivores combined with bottom-up effects of the vegetation can retard vegetation succession in these salt marsh systems for several decades.

Herbivory along a productivity gradient

As primary productivity increases during salt-marsh succession (Olf et al. 1997, Van Wijnen and Bakker 1997, Van Wijnen and Bakker 2000) the successional stages we studied can be regarded as a productivity gradient. The exploitation theory (Fretwell 1977, Oksanen et al. 1981, DeAngelis 1992) predicts that herbivore density and the amount of biomass removed should increase with primary productivity. At highly productive sites, herbivore density should settle to a constant level due to carnivore control of the herbivore population but the biomass removed by the herbivores should continue to increase (Oksanen and Oksanen 2000). In the present study, consumption of hares and geese increased with primary production. However, in the highly productive end of the productivity gradient, the herbivore numbers and consumption declined. As carnivores are lacking on this island, the decrease in plant quality as forage for the herbivores is thought to explain the decreasing numbers as stated in the "quality threshold hypothesis" (Van de Koppel et al. 1996, Olf et al. 1997, Huisman et al. 1999). The highest consumption was, therefore, found at sites of intermediate productivity and was low at sites of both low and high productivity. Both theories predict that consumption to production ratio will peak at sites of intermediate productivity, reflecting the impact of herbivores on the vegetation. The top-down effects of herbivores on the vegetation are predicted to decrease at high levels of productivity due to predator control of the herbivore

population or decreasing plant quality as food for the herbivores. In contrast to the predictions of both models, we found that sites of intermediate productivity, which experienced the highest grazing pressure, experienced the smallest effects of herbivory on vegetation composition. We argue that at these sites, the composition of the vegetation was not controlled by herbivores, but was bottom-up regulated by the vegetation itself. Top-down control of the vegetation was found at both sites of low and high productivity, where releasing the vegetation from grazing resulted in changes in species composition and accelerated succession.

In contrast to the exploitation theory, we showed that next to top-down effects, bottom-up effects can play an equally important role in explaining variation in herbivore density across a productivity gradient. Neither the exploitation theory nor the quality-threshold hypothesis can be used to predict where the largest effects of herbivory occur along this small-scale gradient of primary productivity that we studied. The intensity of herbivory does not necessarily predict the importance of herbivory in structuring plant communities. To understand herbivore effects along productivity gradients, the selectivity patterns of the herbivores and the bottom-up effects of plants on these interactions need to be considered.

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APPENDIX A

A table showing the shift in plant species composition in the high salt marsh enclosures is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-049-A1.

APPENDIX B

A table showing the shift in plant species composition in the low salt marsh enclosures is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-049-A2.